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New species of fossil nonmarine molluscs from Western Australia and evidence of late Quaternary climatic change in the Shark Bay district

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Abstract

The new species *Coxiella roeae* sp. nov. (Prosobranchia: Hydrobiidae), *Bothriembryon gardneri* sp. nov., *B. consors* sp. nov., *B. douglasi* sp. nov. and *B. ridei* sp. nov. (Stylommatophora: Bulimulidae) are described and figured. All occurrences are believed to be of Pleistocene age.

Coxiella roeae sp. nov. was obtained from lacustrine deposits in the Beermullah district and represents the first fossil species to be recorded for the genus.

The four new species of *Bothriembryon* snails come from fossil soils in the Point d'Entrecasteaux and Shark Bay districts. Those from the former locality, *B. gardneri* sp. nov. and *B. consors* sp. nov., are related ancestrally to living species. The two Shark Bay species, *B. douglasi* sp. nov. and *B. ridei* sp. nov., have no known living descendants. Their extinction, and the apparent subsequent appearance of camaenid snails in the district, are interpreted as evidence of a period of severe regional aridity during the late Pleistocene.

Introduction

This paper describes five new species of molluscs, one freshwater and four terrestrial, from the fossil collections of the Western Australian Museum (WAM) and the Field Museum of Natural History, Chicago (FMNH). The material studied came from three widely separated areas in southwestern Australia (Fig. 1).

Coxiella roeae sp. nov. was obtained in sediments collected from wells, seismic boreholes and other shallow excavations in the Beermullah district, 80 km north of Perth, by Mrs. R. Roe, of "Benalong", Beermullah.

From 1941 to 1976, fossil snail shells have been obtained by a number of collectors from exposures, both natural and man-made, of lithified fossil soils associated with aeolian calcarenite at Point d'Entrecasteaux on the coast of Western Australia south-southeast of the town of Northcliffe. The deposit contains at least eight different species of land snails, of which two, *Bothriembryon gardneri* sp. nov. and *B. consors* sp. nov., are described below.

Collections of land snails from widely dispersed fossil soils in the Shark Bay district, resembling the Depuch Formation, have been found to contain two species of *Bothriembryon* distinct from any now living. These species, which appear to be allopatric, are described as *B. douglasi* sp. nov. and *B. ridei* sp. nov.

A comparison of what is known of modern and fossil land snail distributions in the Shark Bay district suggests that a period of glacioeustatic low sea levels during the late Pleistocene was marked by the extinction of two *Bothriembryon* species and the subsequent local establishment of up to four species of arid-adapted camaenid snails. These apparent faunal changes are considered to reflect a regional climatic shift towards increased aridity. A relative climatic amelioration appears to have eventuated in the wake of the Flandrian (Holocene) transgression, possibly reflecting the strengthening of maritime influences in the area.

Systematic descriptions

Class Gastropoda
Subclass Prosobranchia
Order Mesogastropoda
Superfamily Rissoacea
Family Hydrobiidae

Genus *Coxiella* E. A. Smith, 1894.

Coxiella Smith, 1894. *Proc. malac. Soc. Lond.* 1: 98.
Coxiella Smith; Ludbrook, 1956. *Trans. roy. Soc. S. Aust.* 7: 41 (with synonymy).

Type species (by original designation): *Truncatella striatula* Menke.

From consideration of the shell characters, *Coxiella* has been referred to a diversity of families, e.g., Hydrobiidae subfamily Truncatellinae (Thiele 1931; Macpherson 1957), Coxiellidae (Iredale 1943), Truncatellidae (Cotton 1959; McMichael 1967) and Assimineidae (Ludbrook 1956). Living animals of *C. striatula* have been examined by Dr. G. M. Davis of Philadelphia who states (pers. comm., May 1972) that, in characters of the head-foot morphology, mode of progression, form of the eyes and tentacles and the radula, they show affinity with the Hydrobiidae and not the Truncatellidae; clarification of the subfamily position requires further study.

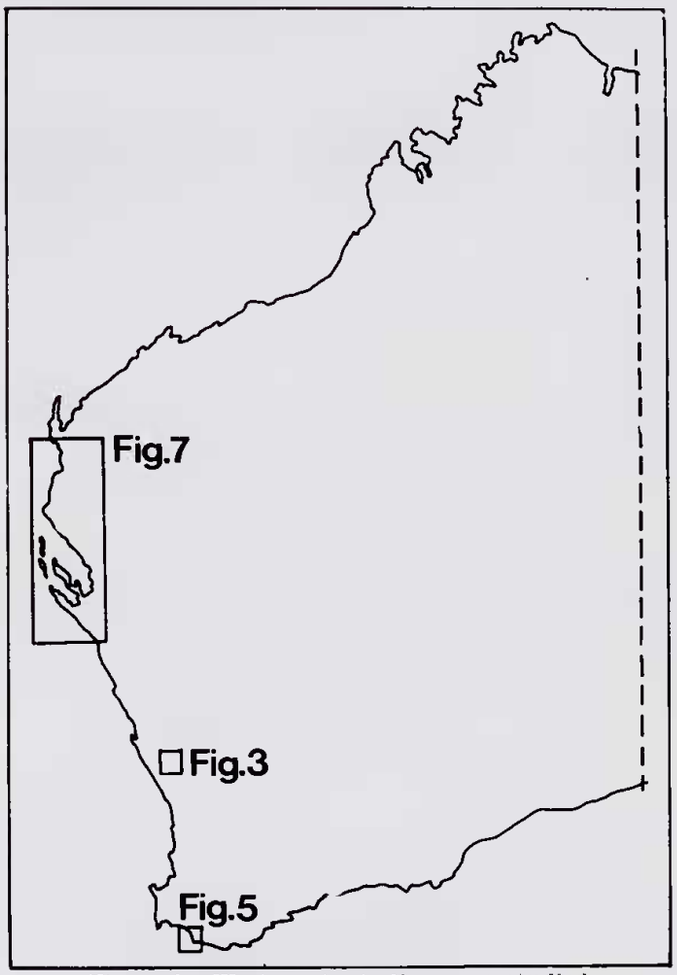

Figure 1.—Western Australia, areas studied.

Coxiella roeae sp. nov.
(Fig. 3)

Material. Holotype WAM 73.4. Paratypes WAM 73.5 (40 shells). Other topotypic reference material WAM 73.6, 73.7, 73.8, 73.9 (5 560 shells). All of this material was collected originally as a single sample.

Type locality. Beermullah, Western Australia. Lat. 31° 11' S, long. 115° 42' E. "Benalong" bore at northern part of Swan Location 5261, about 0.5 km east of Location 2680, ("Pin Pin"); 4.6-4.9 m below ground surface (Fig. 2).

Diagnosis. A medium-sized *Coxiella* up to 17 mm high, of somewhat variable form, elongate-conical or turriculate, with height about twice the maximum diameter. Protoconch smooth, paucispiral, either present or absent through decollation, in which case a septum is formed. Whorls convexly rounded, flattened, shouldered or carinate; sometimes cingulate above the periphery, with sutures impressed or incised. Sculpture of irregular, colabral growth rugae and very fine, close, spiral striae, becoming obsolete on the base and occasionally entirely absent. Umbilicus present, small in juveniles, becoming wide (for the genus) in mature shells. Aperture ovate to quadrate, according to the degree of carination; often with persistent yellow-brown pigmentation within. Shells white externally.

Description of holotype. Shell of medium size, elongate-conical, of 7.8 whorls in a height of 9.6 mm, maximum diameter 5.5 mm. Apex intact, protoconch smooth, paucispiral; spire whorls convexly rounded, the last whorl slightly flattened, sutures impressed. Sculpture of irregular, colabral growth rugae and very fine, close, spiral striae, becoming obsolete on the base. Umbilicus open, small. Aperture ovate, oblique and continuous, the columellar lip everted; faintly yellow-brown within. Shell white externally.

Observations. Of the described species of *Coxiella,* (Macpherson 1957), the fossil species is closest in general shell proportions to *C. pyrrhostoma* (Cox), though not attaining the height of that species (17 against 20 mm). Other similarities are the presence of contrasting pigmentation within the aperture and the spiral striation. Some rugose, shouldered or cingulate shells of *roeae* recall specimens of *C. glauerti* Macpherson from the Esperance-Israelite Bay district. Examination of a range of specimens from that area collected since Macpherson's revision of the genus suggests to the writer that *glauerti* may be no more than a localised gerontic form of *pyrrhostoma.*

C. roeae differs markedly from *pyrrhostoma* and most other species of *Coxiella* in the relatively late onset of decollation and also in the limited extent to which this is usually manifest. This is shown among the fossils by the presence of a substantial proportion of mature shells having either intact or very slightly decollate apices. In *pyrrhostoma* by contrast, decollation appears to occur early in growth when the shell is 4-5 mm high and recurs subsequently a number of times. Juvenile, non-decollate shells of *pyrrhostoma* have a subcylindrical form in contrast to the ovate-conical form of young *roeae.* Occasional shells of *roeae* exhibit a more extensive decollation, comparable to that of extant species. Carination of the whorls in a proportion of shells distinguishes *roeae* from all other congenors. The new species is considerably more variable in shell characters than any other *Coxiella*; however the extreme forms are connected by intermediates and all are considered to represent a single species. The paratype series, a selection of which is illustrated (Fig. 2C-N), demonstrates this variation.

The carinate forms of *C. roeae* bear a remarkable resemblance to shells of *Pyrgula barroisi* Dautzenberg (Truncatellidae) from the Sea of Galilee, figured by Tchernov (1975, p. 156, Figs. 5, 6, 9).

The species is named after Mrs. R. Roe, who presented to the Western Australian Museum all of the material and collecting data utilised in this study.

Geographic range. The present species has been collected by Mrs. Roe from spoil from a series of bores, wells, seismic shotholes and other shallow excavations within 12 km to the south and east of the type locality and from a surface outcrop on the eastern side of Beermullah Lake some 8.5 km to the east. The positions

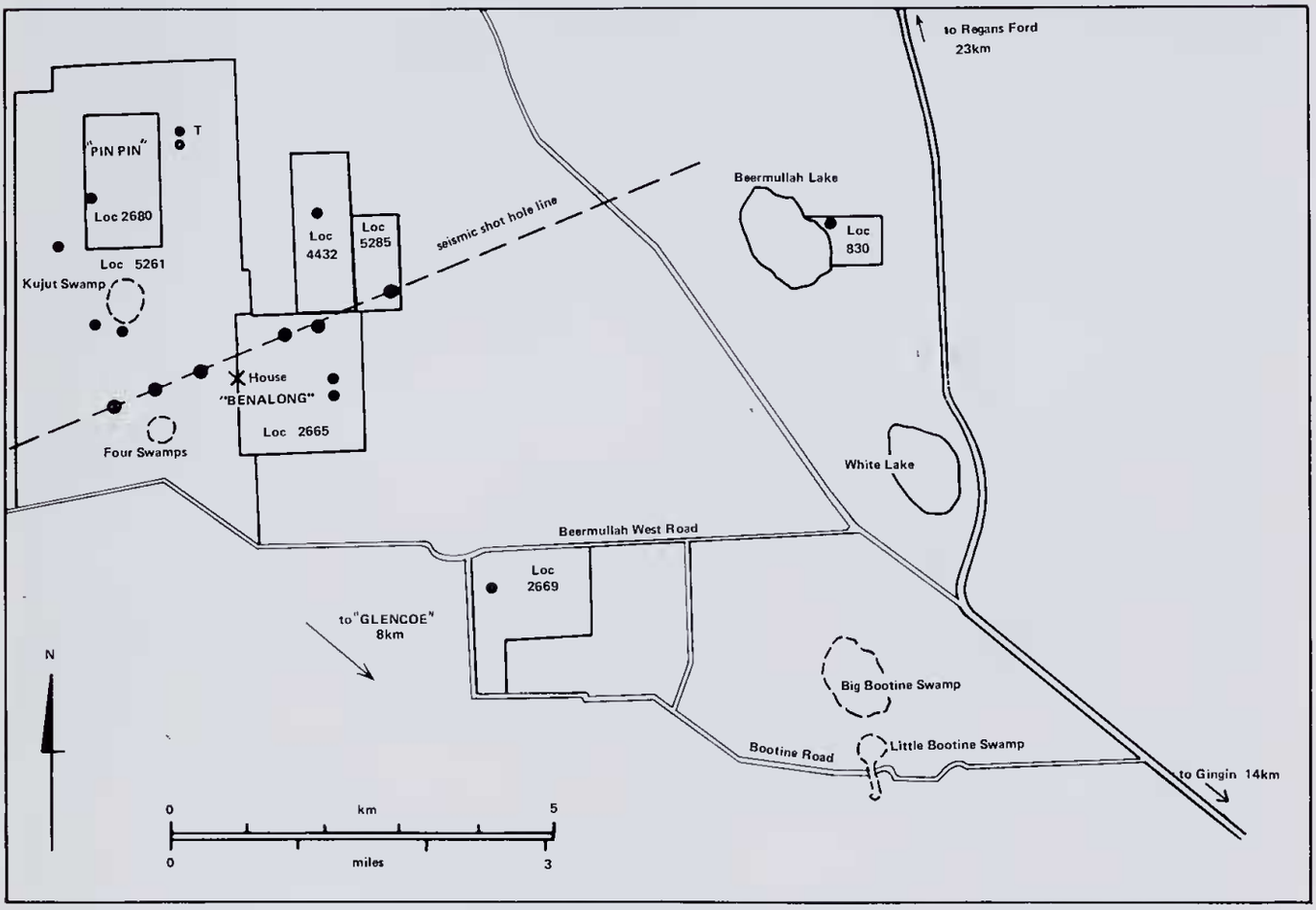

Figure 2.—Beermullah district. *Coxiella roeae* localities. Type locality T.

of these localities are shown in Fig. 2; the greatest depth sampled was 13.7 m below the ground surface. Hosking and Greave (1936, p. 106) report "hard compact limestone containing small mollusc shells of presumably Tertiary age" from near "Glencoe" homestead, Beermullah. This property, now known as "Mirilla", lies about 8 km southeast of known occurrences of *C. roeae* and may contain an extension of the same *Coxiella* beds. The data suggest that one or more extensive lakes may have occupied the area at the time of deposition. The presence of occasional associated fossil shells of the pond snail genera *Physastra* and *Gyraulus* (e.g. WAM 73.10, 71.984) with *C. roeae* indicates that these water bodies were more likely to have been fresh rather than saline at the time of deposition.

Stratigraphic range. The precise age of the present material cannot as yet be determined but marine mollusc shells (WAM 73.98-104, 73.106-7) from a bore on Swan Location 2680 ("Pin Pin", Fig. 2), close to the type locality of *C. roeae* but from between 27.4-36.6 m below the ground surface are, in the writer's view, of probable Pliocene age. If so, then the overlying lacustrine beds containing *C. roeae* were probably laid down during the Pleistocene. Apart from late Quaternary deposits around Lake Eyre, South Australia, containing fossils of the extant *C. gilesi* (Angas) (Ludbrook 1956; King 1956), little has been established of the geologic history of the genus.

Subclass Euthyneura
Order Stylommatophora
Superfamily Bulimulacea
Family Bulimulidae

Genus *Bothriembryon* Pilsbry, 1894.

Bothriembryon Pilsbry, 1894. *Nautilus* 8:35-36.
Bothriembryon Pilsbry; Kendrick and Wilson, 1975. *Rec. West. Aust. Mus.* 3:312 (with synonymy and redescription).

Type species (by original designation): *Bulimus melo* (Quoy and Gaimard) = *Helix melo* Quoy and Gaimard.

Bothriembryon gardneri sp. nov.
(Fig. 4, A-E)

Material. Holotype WAM 70.1603a. Paratypes WAM 70.1603b and c, 2 shells; 66.794a and b, 2 shells embedded in a laminar piece of brown calcarenite; 66.798a, h and w, 3 shells; FMNH 194694/3, 3 shells. Other reference material WAM 70.1603d to p, 13 topotypes; 66.795, 1 shell in hard, brown calcarenite; 66.796, 2 shells in hard, brown calcarenite; 66.797, 2 shells in a large, laminar piece of brown calcarenite; 66.798, 18 complete and 31 fragmentary shells; 62.196, 1 shell in brown calcarenite; 62.197, 1

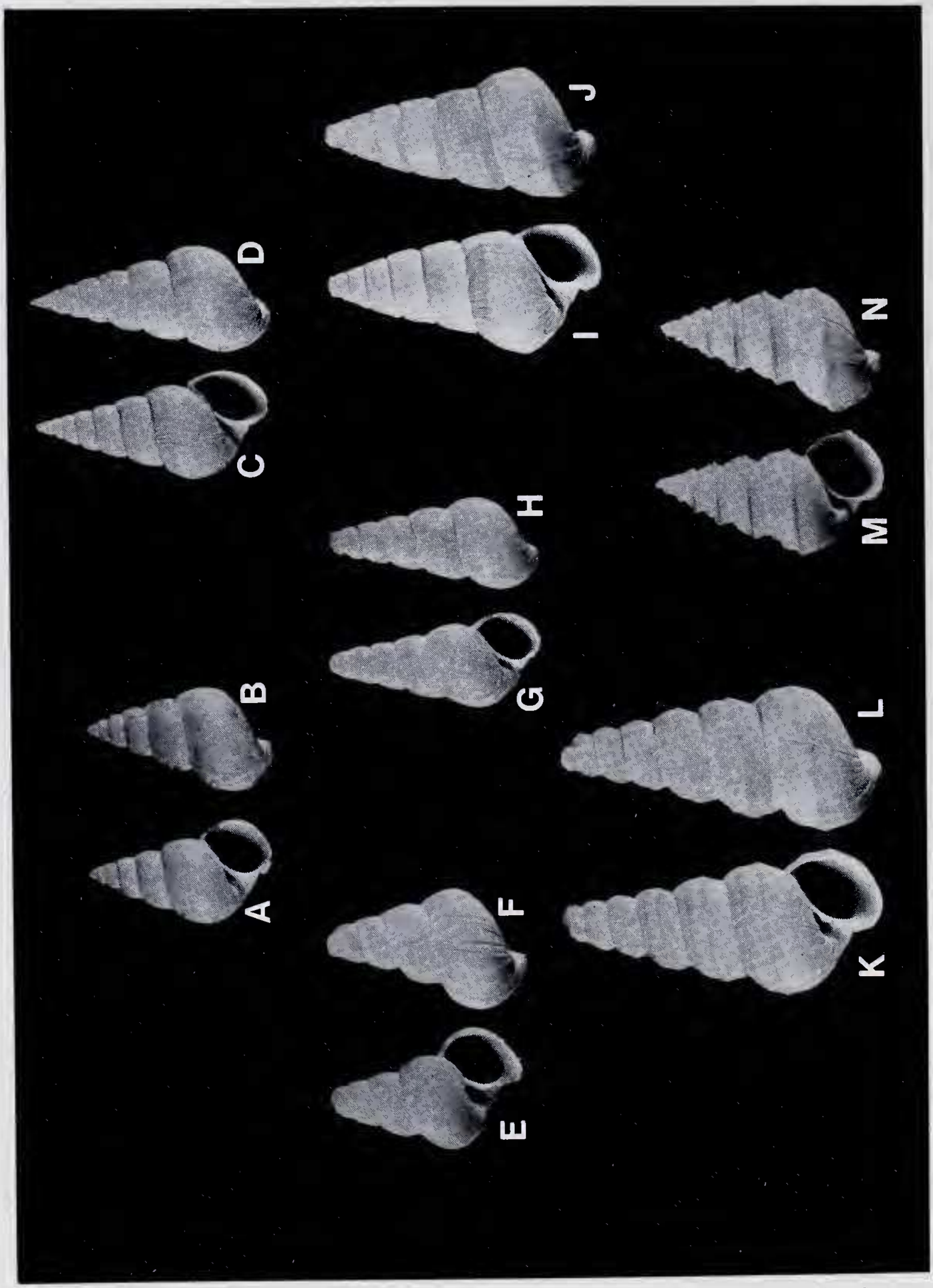

Figure 3.—*Coxiella roeae* sp. nov. A, B.-Holotype, WAM 73.4. C.-N.—Paratypes, 73.5 a-f. All x 3.

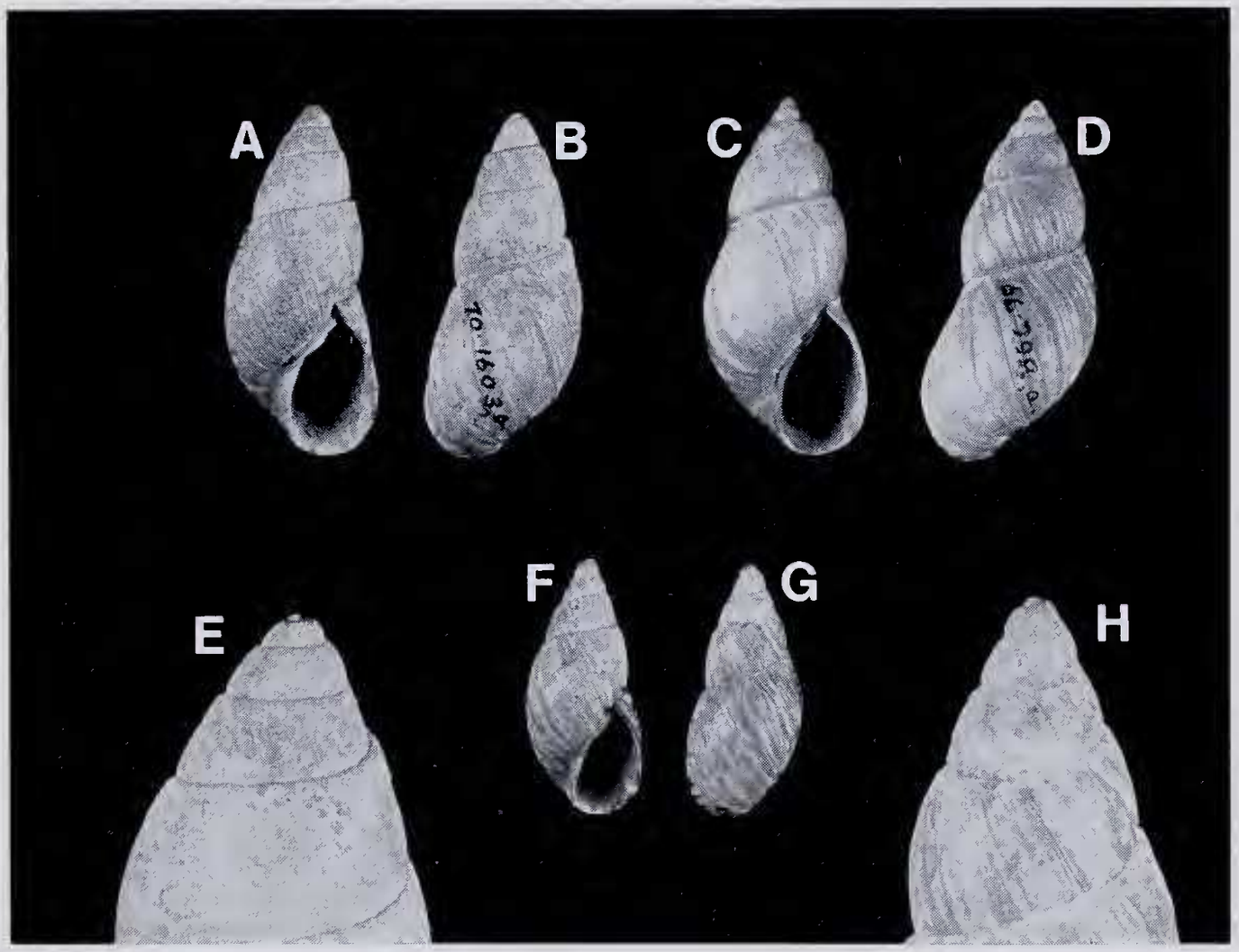

Figure 4.—*Bothriembryon gardneri* sp. nov. A, B, E.—Holotype, WAM 70.1603a C.-D.—Paratype 66.798a. *Bothriembryon consors* sp. nov. F.-H.—Holotype, 72.421a E. and H. x 3; all others x 1.

shell filled with brown calcarenite; 65.33, 2 shells; 65.34, 3 shells; 65.480, 1 shell; 70.900, 10 shells; 72.420, 32 shells; 73.253, 1 deformed shell, probably of this species; 73.254, 1 shell; 75.860, 2 shells; 9881, 2 shells in brown calcarenite: FMNH 182298, 7 shells.

Type locality. Point d'Entrecasteaux, Western Australia. Shallow quarry on crest of low ridge of calcarenite on north side of track from Windy Harbour to Salmon Beach. The site is located 3.5 km on a bearing of 32° from the Point d'Entrecastreaux lighthouse. Lat. 34°49'14"S, long. 116°00'52"E (Fig. 5).

Diagnosis. A large, robust *Bothriembryon*, elongate-ovate, up to 45 mm high, with a height usually greater than twice the maximum diameter and spire height more than half the total height. Whorls convex, about 5.7 in a height of 40 mm, sculpture of strong, colabral growth rugae, generally without spiral granulation. Protoconch of 2.1-2.3 slightly convex whorls, dome-shaped; sculpture fine, mainly reticulate over the first 1.5 whorls and tending to become axially aligned or wrinkled over the abapical portion, where weak axial rugae may also develop. Traces of whitish axial flames are sometimes apparent on the abapical portion of the protoconch.

Description of holotype. Shell large, robust, of 6 whorls in a height of 43.5 mm, maximum diameter 19.5 mm, height of spire 24 mm. Whorls convex, suture impressed and lightly crenulated; sculpture of colabral growth rugae, concentrated below the suture; spiral sculpture absent. Umbilical fissure small. Parietal callus thick, columella concave, thick and reflected. Protoconch dome-shaped, of 2.1 whorls, bearing a fine axially-reticulate sculpture, which becomes progressively more axial on the abapical portion, where weak axial rugae, anticipating the teleoconch sculpture, also appear. The cavity of the shell contains a friable, cream calcarenite.

Observations. Of the described species of *Bothriembryon* from Western Australia (Iredale 1939), *B. gardneri* most resembles *B. fuscus* Thiele from the south coastal Karri forests between Torbay and Walpole. In the shape, size and sculpture of the protoconch, the two species are quite similar; furthermore in each a weak axial flame pattern can be detected occasionally

on the abapical extremity of the protoconch. The two species differ essentially in features of the teleoconch. The fossil species has a rather more elongate shell than *fuscus;* though attaining a slightly greater height than the living species (45 mm against 43 mm), *gardneri* does not reach the maximum width of *fuscus* (19.5 mm against 21 mm). The spire height of mature shells of *gardneri* invariably exceeds the aperture height, whereas in *fuscus* these dimensions are about equal, as Iredale noted. In details of the sculpture, the two species also differ. Axial growth rugae are much stronger in *gardneri* and spiral granulation is generally absent; traces of this feature may be detected under magnification on an occasional shell. Fine spiral granulation and (sometimes) striation ornament the spire whorls of *fuscus*. These occur on the shell proper and are not mere periostracal features. A Field Museum paratype from the Pt. d'Entrecasteaux cliff near the lighthouse shows traces of a wide, axial flame pattern on the teleoconch, such as occurs on some shells of *fuscus*.

This comparison of *B. gardneri* and *B. fuscus* shows that the two share a range of common characters and probably are closely related. Possibly the former stands in an ancestral position to the latter. If so, then the direction of morphologic change has tended toward a shorter, more ovate shell with fine spiral granulation in lieu of strong axial rugae. The presumably non-adaptive protoconch characters have remained unaltered over this time.

Fossil snails associated with *B. gardneri* include two congenors, one of which, *B. consors* sp. nov., is described below, as well as species of *Paralaoma,* and *Magilaoma* (Punctidae), *Pernagera* and one other charopid (Charopidae) and an undescribed assimineid (A. Solem, pers. comm., Sept. 1976). This assemblage suggests a humid, well-vegetated, probably forested environment at Point d'Entrecasteaux at the time of deposition, in contrast to the exposed coastal heath that presently characterises the area.

The species is named after Mr. G. Gardner of Northcliffe, who introduced the author to the type locality and assisted in the collection of the type material.

Geographic range. Bothriembryon gardneri is known only from the type and adjacent localities at Point d'Entrecasteaux, within 4 km of the lighthouse (Fig. 5). The material has been collected from natural and man-made exposures of fossil soils occurring on and beneath the surface of an elevated ridge of aeolian calcarenite, now truncated by a prominent sea cliff.

Stratigraphic range. No direct evidence of age for the calcarenite deposits at Point d'Entrecasteaux is available but, by analogy with similar formations in south-western Australia (Lowry 1967), a Pleistocene age is assumed. The uppermost fossil soil, containing abundant land snail shells, is generally well lithified and underlies a thin, brown, surface (possible deflated) quartz sand. A Pleistocene age for the fossils appears probable.

Bothriembryon consors sp. nov.
(Fig. 4, F, H)

Material. Holotype WAM 72.421a. Paratypes WAM 72.421b to e, j and k, 6 shells; 70.901a and b, 2 shells; 70.1602d, 1 shell. Other reference material WAM 70.1602a to c, e to g, i to m, o to q, 14 shells.

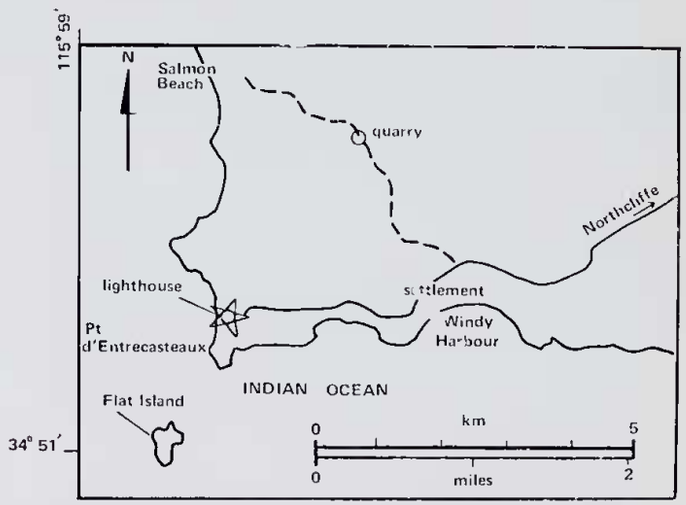

Figure 5.—Point d'Entrecasteaux and Windy Harbour. Quarry is type locality of *Bothriembryon gardneri* and *B. consors.*

Type locality. Windy Harbour, Western Australia. Shallow quarry NE of lighthouse beside track to Salmon Beach. The site is located 3.5 km on a bearing of 32° from the Point d'Entrecasteaux lighthouse. Lat. 34° 49′ 14″ S, long. 116° 00′ 52″ E (Fig. 5). This is the same place as the type locality of *Bothriembryon gardneri,* cited above.

Diagnosis. A medium-sized, robust *Bothriembryon,* elongate, up to 32 mm high, with a height about 2.1 times the maximum diameter; spire height slightly more than half the total height. Whorls gently convex, about 5.5 in a height of 30 mm; sculpture of fine, close, colabral growth lines crossed by fine spiral granulation, concentrated below the suture and becoming obsolete on the last whorl. Traces of narrow, brown and white axial striping are visible on some shells. Protoconch of 1.9 to 2.2 whorls, elevated, somewhat tumid, sculpture finely punctate with or without a weak axial alignment and becoming very finely axially wrinkled on the abapical extremity; pale axial flames present on the second whorl.

Description of holotype. Shell medium-sized, elongate, of 5.3 whorls in a height of 29.9 mm, maximum diameter 13.8 mm, height of spire 16.0 mm. Whorls gently convex, suture impressed and finely crenulated; sculpture of fine, close, colabral growth lines crossed by fine spiral granulation, concentrated below the suture and becoming obsolete on the last whorl. Columella slightly concave and reflected over a minute umbilical fissure. The teleoconch retains faded, narrow, brown and white axial striping. Protoconch elevated, slightly tumid, of 2.1 convex whorls bearing fine reticulate-punctate sculpture, which becomes axially wrinkled near the

abapical extremity; pale axial flames present on the second whorl. The cavity of the shell contains a friable, cream calcarenite.

Observations. From the combination of an attenuate shell, axially striped and with weak spiral granulation and a protoconch patterned with axial flames, it appears that the affinities of *Bothriembryon consors* lie with a group of species from south coastal districts typified by *B. kingii* (Gray). Shells of this general form occur from the vicinity of East Mt Barren westward to the Meerup River some 20 km north of Point d'Entrecasteaux, being represented by the species *maxwelli* Kobelt, *jacksoni* Iredale, *notatus* Iredale as well as *kingii*. The field relationships and precise differentiation of these species await clarification but examination of a range of recently collected material in the Western Australian Museum suggests that there is much intergradation in shell characters. Whether they represent one wide-ranging, variable species or several has yet to be demonstrated conclusively, but despite a generalised resemblance, the fossil species, *consors*, does not closely correspond to shells from any part of this series. Such similarities as can be seen are more noticeable with the attenuate shells that occur from Albany eastward and least of all with the wide, ovate shells that characterise the western end of the series.

In the ratio of height to maximum diameter, *consors* resembles shells of the type population of *B. kingii* from Albany, but differs in other characters. The fossil attains 5.5 whorls in a height of 30 mm, whereas *kingii* reaches only about 22 mm for this degree of coiling. The protoconch of *consors* is larger, more tumid, more finely sculptured and shows less axial alignment of the sculpture than typical *kingii*. Shells of *B. jacksoni* from the Walpole-Nornalup National Park are relatively wide with a height: maximum diameter ratio of 1.8:1, attaining 5.5 whorls in 27 mm; protoconch sculpture tends to be closer to that of *consors* than *kingii* but the teleoconch characters diverge markedly. Throughout the entire modern *kingii* series, the shells tend to be thin and fragile, even where obtained from calcareous coastal soils. By contrast, the shells of *consors* are all robust, some exceptionally so. This contrast between the two species applies to specimens from similar substrates and may represent more than a simple edaphic response. The differences in shell characters between *consors* and the modern *kingii* series (*sensu lato*) indicate that the group has undergone some morphologic divergence during the Quaternary. This may have been greater in the western part of the range, with the development of a wider, ovate form of shell. An overall trend within the group seems to have been the evolution of a relatively thin shell.

B. gardneri and *B. consors* contrast strongly in characters of the teleoconch. The former and larger species has about 5.7 whorls in a height of 40 mm, the latter about 5.5 spirally granose whorls in only 30 mm. The protoconchs of the two species differ in the number of whorls, degree of elevation, sculpture and pattern.

Geographic range. *Bothriembryon consors* is known only from the type and adjacent localities at Windy Harbour (= Point d'Entrecasteaux) within 4 km of the lighthouse (Fig. 5). The localities parallel those for *B. gardneri*, both species occurring together in the same fossil soils at Point d'Entrecasteaux. The name *consors* alludes to this association.

Stratigraphic range. As for *B. gardneri*, probably Pleistocene.

Bothriembryon douglasi sp. nov.
(Fig. 6, A-E)

Material. Holotype WAM 66.1036a. Paratypes WAM 66.1036b, c, 2 shells; 68.1434c, d, g, j and o, 5 shells. Other reference material, WAM 66.1036d to f, 3 shells; 68.1434a, b, e, f, h, i, k to n, 10 shells.

Type locality. Sea cliff at the Carrarang-Tamala boundary fence, Edel Land, Shark Bay, Western Australia. Lat. 26° 32′ 26″ S, long. 113° 26′ 42″ E; from within the top 7.5 m of the cliff (Fig. 7).

Diagnosis. A large *Bothriembryon*, ovate-conical, up to 35 mm high, height about 1.7 times the maximum diameter and attaining about 5.5 whorls in a height of 27 mm. Spire about half the total height or less; sculpture of fine, irregular growth lines crossed above the periphery by weak spiral granulation. Columella thin; umbilicus small, open. Protoconch bluntly rounded, of 2.1 to 2.4 wide, convex whorls, sculptured with fine, close irregular axial wrinkles. Protoconch apparently of one colour, slightly darker than the teleoconch.

Description of holotype. Shell large, ovate-conical, of 6.0 whorls in a height of 34.2 mm, maximum diameter 19.6 mm, height of spire 17.0 mm. Whorls convex, suture impressed and edged with a weak groove, base evenly rounded; sculpture of growth lines crossed above the periphery with fine, spiral granulation. Columella thin, reflected, partly obscured by matrix; umbilicus small. Protoconch of 2.1 whorls, rather worn but retaining traces of fine, close axial wrinkling; slightly darker than the teleoconch. The type is a dull-white, somewhat worn shell, cracked on the spire and lacking small sections of the outer layer in several places; the exterior carries some thin, pale-brown calcrete and the cavity is filled with a hard, pale-brown quartzose calcarenite.

Observations. In the form of the teleoconch and the sculpture and deeper shading of the protoconch, only one species, *B. distinctus* Iredale from the Balladonia district (Iredale 1939) shows any significant resemblance to *B. douglasi*. The similarity is less obvious with larger fossils, such as the type of *douglasi*, but more so with smaller shells, such as those from the "Zuytdorp" locality (Fig. 7), which are about the same size as mature specimens of *distinctus*. Spiral granulation on the teleoconch is a little stronger in *distinctus* and there is a size difference in the protoconch; that of *douglasi* ranges from 2.1 to 2.4 whorls, *distinctus* from 1.7 to 2.1 whorls. These differences, together

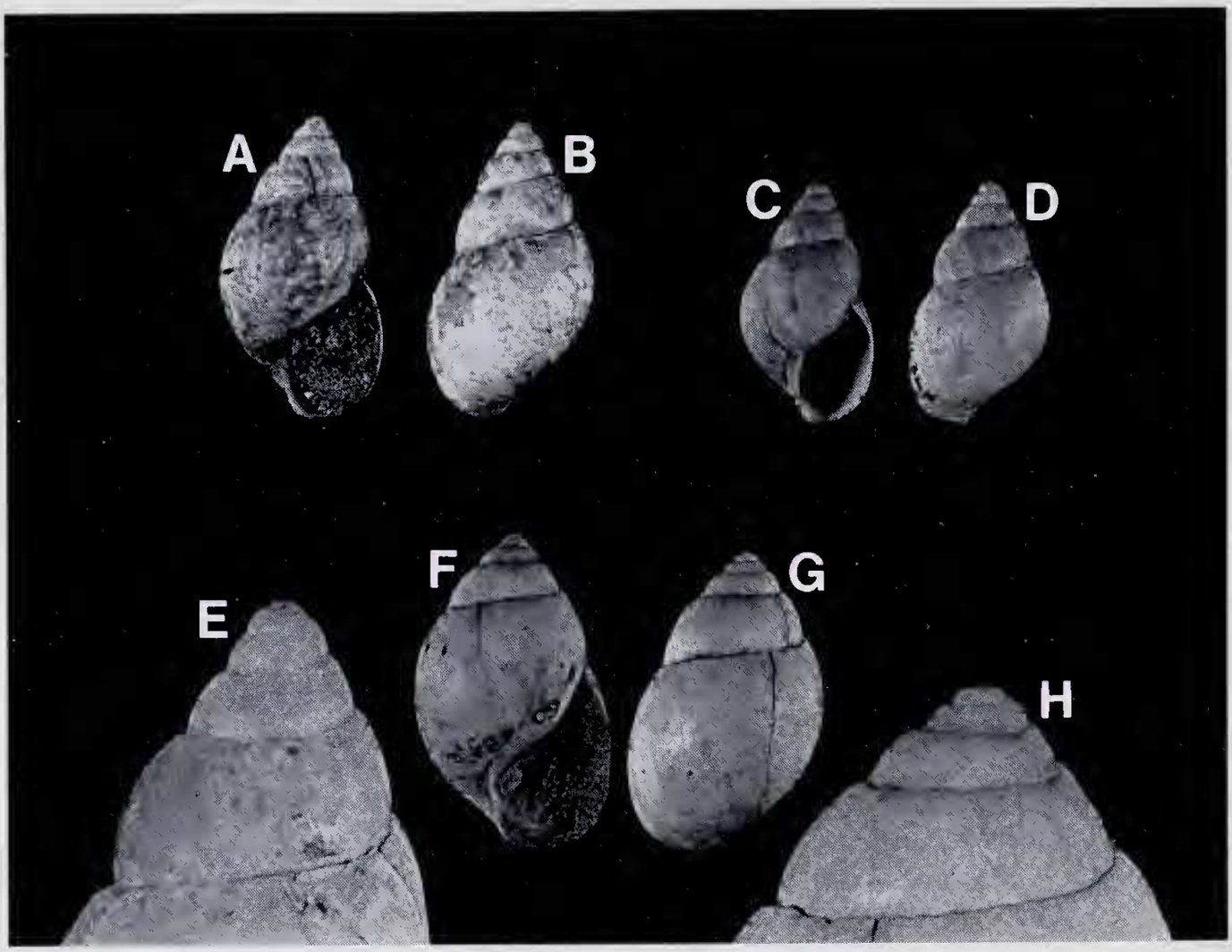

Figure 6.—*Bothriembryon douglasi* sp. nov. A,B.—Holotype, WAM 66.1036a. C.-E.—Paratype 68.1434d. *Bothriembryon ridei* sp. nov. F.H.—Holotype, 60.434a. E and H x 3; all others x 1.

with the remoteness of the two geographic ranges (over 1 000 km apart) suggest that the two species have been differentiated for an appreciable time.

At the type locality, the new species is associated with fossils of *B. costulatus* (Lamarck) (WAM 66.1037); a shell, probably also of Lamarck's species has been collected from a fossil soil at the "Zuytdorp" site (WAM 68.563) (Kendrick and Wilson 1975).

The new species is named after Mr. A. M. Douglas, who collected the specimens from the "Zuytdorp" locality, employed in this description.

Geographic range. *Bothriembryon douglasi* is known only from the type locality and from a similar position on the coastal cliffs at the site of the "Zuytdorp" wreck, 70 km further south.

Stratigraphic range. At both of the known localities, shells of *B. douglasi* occur in fossil soils similar to the Depuch Formation of the Shark Bay district (Logan *et al.* 1970). Specimens are associated with brown, quartzose, calcarenites; some from the type locality also bear thin, hard crusts of light brown calcrete. A Pleistocene age seems probable for these lithified fossil soils.

Bothriembryon ridei sp. nov.
(Fig. 6, F, H)

Material. Holotype WAM 60.434a. Paratypes WAM 60.434b, d, e, 3 shells; 66.660a, 74.531a. Other reference material WAM 60.434c, e to p, 13 shells; 65.1158, 1 shell; 66.660b to l, 11 shells; 66.675, 1 shell; 69.1207a to d, 4 shells; 70.1869a, b, 2 shells; 74.531b to h, 7 shells.

Type locality. Western side of Dorre Island, Western Australia; limestone cliffs opposite Disaster Cove. Lat. 24° 59′ 52″ S, long. 113° 07′ 12″ E (Fig. 7).

Diagnosis. A large *Bothriembryon*, ovate-conical, ventricose, up to 40 mm high, height about 1.5 times the maximum diameter and attaining about 6 whorls in a height of 38 mm. Spire less than half the total height; sculpture of fine growth lines with weak spiral granulation present above the periphery but becoming obsolete on the last whorl. Columella thin, umbilicus small. Protoconch of 1.8 to 2.1 whorls,

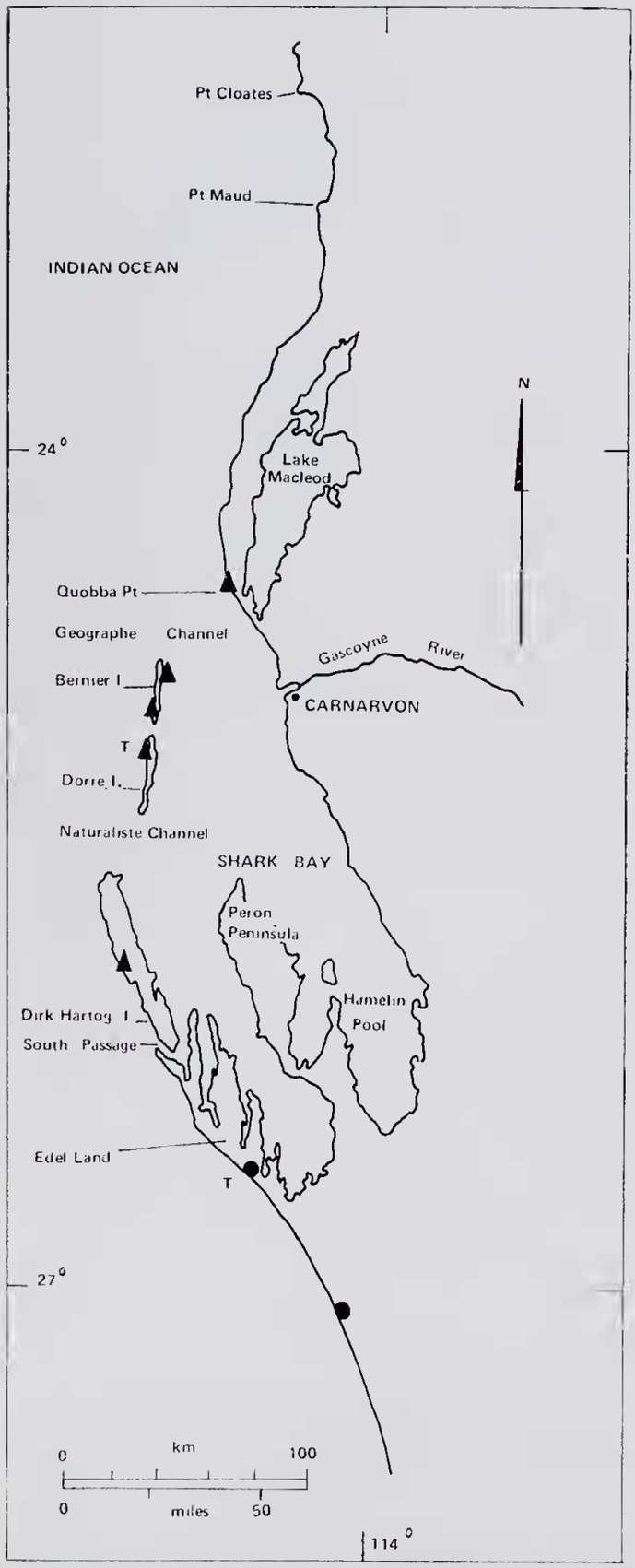

Figure 7.—Shark Bay district. *Bothriembryon douglasi* localities. ● *Bothriembryon ridei* localities. △ Type localities T.

low and wide, sculptured with axial reticulation. Protoconch apparently of one colour, tending to be darker than the teleoconch.

Description of holotype. Shell large, ovate-conical, ventricose, of 5.9 whorls in a height of 36.3 mm, maximum diameter 22.7 mm, height of spire 16.0 mm. Whorls convex, suture impressed; sculpture of fine growth lines crossed by weak spiral granulation above the periphery and becoming obsolete on the last whorl; base evenly rounded. Columella thin, reflected; umbilicus filled with sediment. Protoconch of 2.0 whorls, low, wide, sculpture axially reticulate and strong; of one colour, slightly darker than the teleoconch. Like all the material to hand, the type is a dull white shell lacking other indication of the original colour. It is cracked in several places and part of the outer lip is missing. The cavity is filled with brown calcrete.

Observations. In form and size, *B. ridei* most resembles shells of *B. dux* (Pfeiffer), from the south coast region of Western Australia between about Ongerup and Caiguna. The new species however has a more ventricose shell, on which the spiral granulation is stronger and does not attain the height of the other (41 mm compared with 55 mm for *dux*). The protoconchs of the two species are of similar size but that of *ridei* exhibits a stronger axial component in the sculpture, best exemplified by paratype 60.434e.

The new species is named after Dr W. D. L. Ride, who, whilst Director of the Western Australian Museum, collected the type series and other material of this species.

Geographic range. Occurrences of shells of the present species at the type locality are discussed by Ride (1962, p. 24, 25, pl. 11). Additional occurrences are: Western side of Dirk Hartog Island, 32 km north of the homestead, apparently weathered from the cliff; Bernier Island, eastern coast near Wedge Rock and western coast opposite Red Cliff Point; Quobba Point near "The Blowhole".

Stratigraphic range. The report of Ride (1962) and field data recorded on labels accompanying the above material indicate that *B. ridei* occurs in fossil soils resembling those of the Depuch Formation, overlying the Tamala Eolianite. (Logan *et al.*, 1970). All specimens to hand are associated either with a dense, brown calcrete or indurated quartzose calcarenite. A Pleistocene age seems probable.

Late Quaternary climate in the Shark Bay district.

A comparison of modern and (what is known of) fossil land snail distributions in the Shark Bay district reveals some apparent contrasts which deserve consideration. Assuming that *B. douglasi* and *B. ridei* were broadly contemporaneous, it would appear that, at some as yet undefined stage of the Pleistocene, three species of *Bothriembryon*, all relatively large-shelled, inhabited the district; *ridei* occurred across western and northern Shark Bay and *douglasi* occupied the Edel Land coast (Fig. 7). The

distributions of these two species seem to have been allopatric. The third species, *costulatus*, which is extant (Kendrick and Wilson 1975), coexisted with both fossil species but the shells tended to be larger than modern specimens. The largest known example of *costulatus* (WAM 66.1037g, 6.2 whorls in a height of 30.1 mm) is a fossil from the type locality of *douglasi*. The extinction of two of these species and the size-reduction of the third presumably resulted from adverse environmental change, probably in-increased aridity. Whether this size-reduction applied generally to *costulatus* throughout its range, or featured local extinction and subsequent replacement by selected morphs of reduced size from outside the immediate area, remains speculative. The latter hypothesis is supported by the presence of distinctive, large-shelled populations of *costulatus* inhabiting the littoral fringe between Point Cloates and Point Maud. A shell of this form, from near the northern end of the species' range, was illustrated by Kendrick and Wilson (1975, Pl. IV, Fig. 11).

The Camaenidae, which incorporates the Chloritidae, Xanthomelontidae and Rhagadidae of Iredale (1939), are the principal family of land snails in arid Western Australia from Shark Bay northward, being particularly well developed in the Kimberley region (Wilson and Smith 1975). At least four species represent the family in the Shark Bay district; one in particular, *Rhagada torulus* (Ferussac), is common on Bernier and Dorre Island and also occurs on Dirk Hartog Island and at Quobba and elsewhere on the mainland coast. Species of *Angasella* and *Plectorhagada* occur along the southern and south-eastern littoral and hinterland, while a *Plectorhagada* is present on Dorre Island. This group of snails is currently being studied by Dr A. Solem. Camaenid records are rare in west-coastal districts south of about latitude 27°, the peripheral occurrences in this region being *Angasella abstans* in the lower Murchison and Greenough districts (Iredale 1939 and G.W.K. unpublished notes). *A. abstans* appears to be a relict species with a strongly disjunct distribution, isolated from the main occurrences of the family. It may represent an earlier Pleistocene camaenid incursion into the northern fringe of the humid south-west. The family is absent from the south-western corner of the State, where *Bothriembryon* dominates the land-snail fauna.

No camaenid fossils have been found in association with either *B. douglasi* or *B. ridei*, despite the abundance of modern specimens, notably those of *Rhagada torulus*, at most of the known localities of the latter species *(ridei)*. The few fossil records of camaenids from the

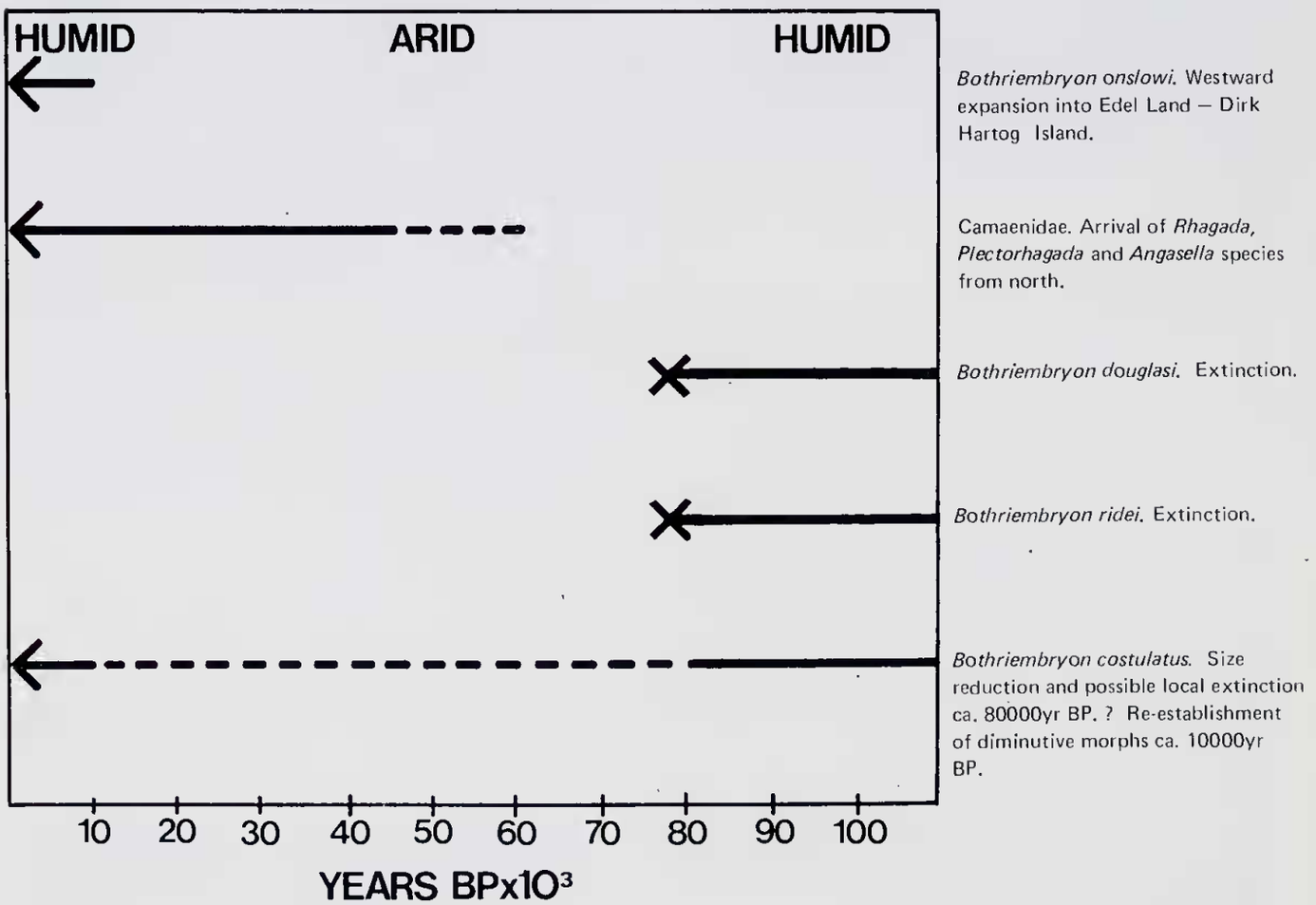

Figure 8.—Conjectural late Quaternary history of *Bothriembryon* and camaenid species in the Shark Bay District.

Shark Bay district (WAM 66.807, 73.85, 73.87) all appear to be of very recent geologic age. Significantly, all are associated with the diminutive, modern form of *Bothriembryon costulatus*, for which Iredale (1939) employed the name *B. minor* Pilsbry (Kendrick and Wilson 1975).

The evidence available from modern and fossil records suggests that the camaenid snails reached the Shark Bay district at some time after the extinction of *B. douglasi* and *B. ridei*. The demise of these two species and the size-reduction of *B. costulatus* are seen as consequences of an environmental change toward greater aridity. It is assumed that the camaenids, being pre-adapted to the drier conditions prevailing in northern areas, would have been favoured by any such change and would have extended their ranges southward and westward into the Shark Bay area. It is noteworthy that camaenids closely related to Shark Bay species are at present living in the country between the Gascoyne River and Cape Range; these may represent the original stocks from which the Shark Bay camaenid populations originated.

The timing of these events cannot yet be established precisely but some inferences can be drawn from the distribution data. Camaenid populations on Bernier and Dorre Islands have been isolated from the mainland since the submergence of the Naturaliste and Geographe Channels during the Flandrian transgression of the sea, some 8 000 year ago (Morner 1971, p. 76). The bathymetry of South Passage between Dirk Hartog Island and the mainland indicates that severance of this island probably occurred a little later. Prior to this, the mainland connections of the Shark Bay "islands" would have been continuous for the entire duration of the last major glacio-eustatic regression of the sea, corresponding to the Wurm-Weichselian glaciation of northern Europe. During this period of global cooling, which became fully assertive from about 80 000 year ago (Broecker and van Donk 1970, Emiliani 1972), sea level fell more than 100 m below its present position (van Andel *et al.* 1967). The camaenid occupation of the Shark Bay district, in particular of the western islands, probably occurred during this time. If so, it may be assumed tentatively that the extinction of *Bothriembryon douglasi* and *B. ridei* marked a transition from (relatively) humid to arid conditions beginning around 80 000 year ago (Fig. 8).

Evidence in support of relative aridity in low and middle latitudes accompanying the reduced global temperatures of the last major glaciation of the Late Pleistocene has been advanced from studies in northern and eastern Australia (van Andel *et al.* 1967; Bowler and Hamada 1971; Dodson 1975), in south-east Asia (Verstappen 1974), the equatorial Pacific (Quinn 1971), tropical South America (van der Hammen 1972) and, in a review of all continents by Williams (1975), indicating a general convergence of views in this direction. Differences between modern and fossil distributions of land snails in the Shark Bay district are consistent with such an interpretation.

Still to be considered is the history of *B. onslowi* (Cox), the second extant species of *Bothriembryon* in the Shark Bay district (Kendrick and Wilson 1975). Fossils to hand are few (WAM 66.278, 66.658, 66.668, 71.225), all being derived from modern soil profiles of young geologic age. Associated fossils include the diminutive, modern form of *B. costulatus* but, as yet, no camaenids. The distribution of *onslowi* around southern Shark Bay, in Edel Land, on Peron Peninsula and Dirk Hartog Island (but not on Bernier or Dorre Islands) suggests that it entered the westernmost part of this range at a time when Dirk Hartog Island was joined to the mainland but when Bernier and Dorre Islands were not. As noted above, this would have been some time after 8 000 year ago. The living colours of *B. onslowi* are shades of a rather intense brown, matching the strongly coloured soils of Peron Peninsula and the south-eastern hinterland of Hamelin Pool. Well-developed cryptic coloration such as this supports the view that the species has had a relatively long association with areas of deeply coloured soils and a more recent presence in Edel Land and Dirk Hartog Island, where soils are pallid.

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